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COMPARATIVE MORPHOLOGY OF DOTHIDEACEOUS AND KINDRED STROMATA

WALTER LEROY BLAIN

(WITH PLATES 1–3)

INTRODUCTION

Parasitic fungi with ascigerous stromata have been variously classified by different authors, and important emphasis has always been placed on the structural characters of the stromata and the relation of the stromata to the host, while asci and spores have been considered less significant.

The object of this paper is to make a comparative study of the stromata and of their relation to their hosts, involving many genera and species of parasitic fungi. Forty-six genera with 85 species, of stromatic fungi, for the most part those with ascigerous stromata, parasitic on leaves and stems, have been examined. The fungi were mainly of the Dothideales but other orders and families showing somewhat kindred structures have been included for purposes of comparison. All of the fungi listed in this paper have been studied quite in detail and the observations on them are given as an appendix to this thesis which is filed in the library of the University of Illinois. The forms studied, many of them type specimens, are to be found in the herbarium of the Botany Department of the same institution.

It is realized that from either a taxonomic or phylogenetic standpoint a study of the life history and general development of the stromata is very desirable but time has not allowed a critical consideration of the taxonomic position of the fungi. Each

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specimen has been accepted under the name assigned to it by others, either by packet labels or in printed articles. In cases where there is a difference in the usage of names by different authors the system of Theissen and Sydow (**17**) has been followed.

In forms as previously described, students have examined, perhaps, a single species, with a preconceived character used in the classification of fungi in mind, and have described the fungus as having this or that character of stroma. In many instances studies have been made with free-hand sections, which of necessity did not reveal the true character of the fungous structure. In the present study serial microtome sections were used, and by examining many species comparative differences or agreements were brought to notice that otherwise would not have been seen. This study of stromatic structure has been helped very much also by the use of Pianeze III b (**21**) as a stain. With this the young stroma or mycelium stains pink or red according to its age; the very old, dense, dark stroma such as is found in clypeate structures and other fungous masses of similar form does not take up this stain. In intermediate cases, between the old dark stage and the young hyaline stage, the mycelium stains green.

In dealing with the various structures in the morphological units involved in this study it has been necessary, for precision and definiteness, to coin some new words which are marked by an asterisk.

THE GENERAL MORPHOLOGY OF STROMATA

The stromata studied consist of one or more of three fundamental parts:

1. The loculiferous region;* the definite part of the stroma in which the locules are borne (PLATE 1, FIG. 24).

2. The extraloculiferous stroma,* usually homogeneous in nature, which is similar in structure to the loculiferous region and extends beyond it (PLATE 1, FIG. 25).

3. The hypostroma, that part of the stroma which lies imbedded in the host below a superficial loculiferous region, or that portion which lies within the host tissue around and external to the loculiferous region (PLATE 1, FIGS. 26 and 24).

* Denotes new words.

The loculiferous region may be either large and complex (PLATE 1, FIG. 24), or very small and simple (PLATE 1, FIG. 27). In its simplest form it is merely a slight accumulation of pseudo-tissue around, above, or below the border of the locule (*Phyllachora Phaseoli*, PLATE 1, FIG. 27). In its more highly developed form it consists of a large and complex stroma in which several to many locules are borne (PLATE 1, FIG. 24). Loculiferous regions may for convenience be subdivided into two categories: (1) the epistroma, external to the host tissue, and (2) the endostroma, which lies imbedded within the host.

The locules are spherical, flask-shaped, ellipsoidal, or angular in shape. In the normal development the pressure on all sides of a locule is the same, but in *Phyllachora* and other genera, due to the unequal development of the locules, they may be irregularly compressed so as to result in cubical, rectangular, or variously angled locules. They vary greatly in size according to the species, some reaching a height of one millimeter, but usually they are much smaller.

Surrounding the locules is a more or less dense layer of stroma, the border.* This varies in density and thickness in different species of fungi. In some instances it consists of a very dark, dense layer of mycelium, so dense that its structure cannot well be made out, while in other cases it is dense and dark immediately surrounding the locules but shades off in the mesostroma into a lighter and looser structure. In some cases it is dark and dense but blends indefinitely into the surrounding mesostroma, in other instances it is formed throughout of nearly hyaline cells. In some species a definite border is lacking, the pseudo-tissue immediately adjacent to the locule being identical in structure with the mesostroma.

The interior of the locules is usually lined with a soft, delicate, hyaline, somewhat gelatinous layer of fine hyphae which are arranged concentrically, constituting the lining * (PLATE 1, FIG. 28).

The hymenium from which the asci develop either occupies the bottom of the locule or extends over a much larger region, sometimes over nearly all of the interior surface of the locule (PLATE 1, FIG. 29). The hymenium of *Dothidea tetraspora*

(PLATE 1, FIG. 30) is especially interesting because of its characteristic mammiliform shape.

The asci, which are of various shapes and sizes, and the paraphyses, if present, usually fill practically all of the space in the locules, but in certain species of fungi there is found between the asci a characteristic pseudoparenchyma. The cells of this pseudoparenchyma are relatively large as they occur among the asci but are smaller near the periphery of the locule. In some fungi there is present at the top of the locule a plug,* composed of pseudoparenchymatous cells, occupying the place where the ostiole ordinarily would be (PLATE 2, FIG. 31).

Frequently the loculiterous stroma possesses a rind, composed of a dense black stroma usually two or three cell in thickness (PLATE 1, FIG. 25). This corresponds in function to the cortical tissue of the higher plants and varies in extent from occurring only on top of the loculiferous region, which is usually the case, to extending entirely around it like a band (PLATE 2, FIG. 32).

No definite ostiole, surrounded by a beak lined with periphyses, as is so typically characteristic of the Sphaeriales, has been found in the study of the fungi involved in this paper except in those fungi which obviously belong to the Sphaeriales. In the Sphaeriales there is a definite perithecium present and the ostiole is formed by a few cells next to the top of the central cavity which disorganize and provide a small, free space into which the adjacent cells elongate, turning upward. The disorganization of the cell walls continues and finally the ostiole is completed. In the dothideaceous fungi studied the opening is formed by a breaking away of the stroma above the top of the locule. In the genus *Phyllachora* the locule often extends upward to form a neck and the opening for the discharge of the spores is formed by the breaking open of the stroma above this neck.

The mesostroma,* that part of the loculiferous region exclusive of the clypeus and locules, is either homogeneous or heterogenous in nature. It falls into one of the following categories: (1) a stroma too dense and dark to reveal its cell structure; (2) typically dothideaceous, *i.e.*, having a palisade-like structure (PLATE 2, FIG. 33); (3) a close weft (PLATE 2, FIG. 34); (4) a loose weft (PLATE 2, FIG. 35); (5) a stroma composed of

pseudoparenchymatous cells of no particular form (PLATE 2, FIG. 36); and (6) of long, hyaline, gelatinous cells (PLATE 3, FIG. 37).

The interlocular region,* the stroma between the locules, is usually of structure similar to that of the mesostroma, but it is often somewhat darker and more dense. Also, due apparently to lateral pressure, it more frequently assumes a pseudoprosenchymatous or even a dothideoid character than does the remainder of the mesostroma.

The clypei, which may be epiphyllous, hypophyllous, or amphigenous, vary in form from a very thin, dense, black stroma to a thick, dense, black structure. Usually the clypeus consists of nothing more than the epidermal cells filled beyond recognition with very dark mycelium. Frequently, however, the cells immediately below the epidermis are also filled with the same kind of stroma resulting in a very thick clypeus. In some instances only certain cells of the epidermis are occupied with the dark hyphae resulting in an imperfect clypeus of very characteristic structure (PLATE 3, FIG. 38). The clypeus varies in extent from barely covering the top of the locule (PLATE 1, FIG. 27) to greatly exceeding the loculiferous region (PLATE 3, FIG. 39).

The extraloculiferous stroma, as a rule, is more dense and darker colored than the loculiferous region, in fact so dense in many cases that its structure cannot well be made out. It is usually of structure similar to that of the loculiferous region and is usually homogeneous. It extends beyond the loculiferous region on either side, sometimes to a great distance (PLATE 1, FIG. 25). Extensive development of extraloculiferous stroma is found in only a few fungi, the greater number of those occurring in the Phyllachorineae. In those species of fungi in which the extraloculiferous stroma occurs above the host tissue it is usually divided into two parts: the covering part or rind and the inner part or mesostroma.

The hypostroma, which serves to anchor the loculiferous region in the host, and for purposes of nutrition, may be considered as of two types: (1) The internal mycelium below a superficial loculiferous region; (2) The stroma which lies imbedded in the host tissue around and external to the loculiferous region. No

absolutely definite line can be drawn between the stroma of the loculiferous region and this latter hypostroma as one merges off into the other.

The hypostroma appears in many different forms. In its simplest form it consists merely of very thin mycelial threads which penetrate the cuticle and extend as haustoria into the epidermal cells and sometimes into the mesophyll (*Actinodothis Perottetiae*, PLATE 3, FIG. 40). A slightly more complex form is where thin mycelial threads penetrate into the host and in certain of the epidermal cells develop so as to form very dark masses of mycelium, *Palawaniella Eucleae* (Fig. 3. Bothalia 1: 17. 1921). More often the hypostroma is located in the mesophyll of the host tissue as: (1) loose intercellular mycelium; (2) as more or less compact masses of mycelium in the host cells, in some instances compressed so as to appear as blocks of stroma, and in other cases packing and swelling the cells, causing them to lose their identity; (3) as subcuticular or subepidermal, sheet-like masses of stroma; (4) as a column-like or knobby protruding foot: and (5) as various combinations of these forms. In certain cases the hypostroma appears to be lacking or very inconspicuous.

THE LOCATION OF STROMATA AS REGARDS THE HOST TISSUE

In recording the location of the stromata, upon or within the host tissue, the plan of Theissen and Sydow, with slight modifications, has been followed. They have recognized five different types, namely: (1) superficial; (2) subcuticular; (3) subepidermal; (4) erumpent; and (5) lying within the mesophyll. In my own work I recognize the following types: superficial, subcuticular, epidermal, subepidermal, erumpent-superficial, and lying within the mesophyll. In the subcuticular type of Theissen and Sydow confusion may arise since the mycelium may not only occupy the space between the cuticle and epidermis but quite frequently also penetrates into the epidermal cells partially or entirely filling them. In order to avoid any confusion I subdivide this type and term as subcuticular, the stroma which is actually confined to the space between the cuticle and epidermis, as epidermal, the stroma which partially or entirely fills the epidermal cells of the host, and as subepidermal, such stromata as

lie below the epidermis but are not at all within it. Because of the tendency of the erumpent forms to spread out fan-like and to appear superficial I call that type "erumpent-superficial" corresponding to the erumpent type of Theissen and Sydow.

THE CELLULAR STRUCTURE OF STROMATA

The loculiferous region is composed of pseudoparenchymatous or pseudoprosenchymatous cells though often so dense and dark that it is difficult to determine accurately the component cells. That part of the loculiferous region comprising the mesostroma has many different cell forms. Fungi possessing a dothideaceous stroma have elongated cells that are usually dark colored, thick walled, and are arranged in a palisade-like manner (PLATE 2, FIG. 33). In a few cases, in *Anisochora Tabebuiae* (PLATE 1, FIG. 25) in particular, the stroma is dothideaceous in structure but the cells are light colored and thin walled. In certain instances the stroma is pseudoprosenchymatous, but does not show a distinct palisade arrangement, nor is it composed of long, parallel-walled cells but of cells that are ellipsoid in form (PLATE 3, FIG. 41). Those stromata that possess a pseudoparenchymatous structure have their cells approximately isodiametrical.

The interlocular region, which is usually dark in color, is made up of pseudoparenchyma or pseudoprosenchyma, and in most cases when composed of the latter is compressed but sometimes its cells are approximately isodiametrical in form.

The border of the locule is composed of light or dark pseudoprosenchyma or pseudoparenchyma, the cells of which are usually somewhat compressed but none show dothideoid structure.

The rind, usually of two or three cells in thickness, is composed of more or less dark pseudoparenchyma or pseudoprosenchyma.

Inside the locule the lining is composed of very thin, hyaline cells which are closely pressed together and arranged in concentric layers. The interascicular pseudoparenchyma and plug are composed of thin-walled, hyaline, isodiametrical cells much larger in the interascicular region than in the plug.

The extraloculiferous stroma is usually differentiated into two parts, the rind and mesostroma, but is frequently so dense

and dark that it appears as a solid stroma and as a result its cell structure is not revealed. The rind, usually very dense, is frequently composed of dark pseudoprosenchyma, and the mesostroma varies in structure, being the same as that of the loculiferous region.

The cellular structure of the hypostroma is quite varied. In those species in which the hypostroma is developed as a foot * this may be dothideaceous. In *Nowellia guianensis* the central part of the foot is dothideoid, the rest pseudoprosenchymatous, while in *Corynelia portoricensis* it is dothideaceous throughout. In other cases it may consist of either pseudoparenchymatous or pseudoprosenchymatous cells which usually are lighter in color the deeper they penetrate into the host tissue. In some instances the foot consists merely of thin-walled, hyaline, mycelial threads which penetrate into the host tissue.

DISCUSSION

The term stroma was first used by Persoon (**14**) who used it to describe the structures on or in which are borne the pyrenocarps in the genus *Sphaeria*. Fuckel (**8**) used the term in the same sense as Persoon and used it in describing the family Dothideaceae. The definition of de Bary (**3**) which has been followed in this paper differs but little from that of Persoon. De Bary considers stroma as a crust or cushion in which ascocarps are developed. Stroma as used in this article may be quite variable in structure, form and color but it is primarily the matrix on which or in which sexual or asexual fructifications are formed.

Fuisting (**9**) was the first to use the term epistroma and he considered it as a hyaline pseudoparenchymatous crust formed in the outer layers of the primary cortex of the host which produces conidia. Under this crust a hypostroma, according to him, is produced later in which perithecia develop. Ruhland (**15**) has used the terms ectostroma and entostroma for these structures following the conception of Fuisting. These terms as used by Fuisting would not fit the Dothideaceae as a whole for there are numerous forms in this family which are not known to produce asexual fructifications. These same terms are used

by Theissen and Sydow to contrast the stroma appearing outside and within the host and it is in this sense that they have been used in this paper.

Many different stages of development of fungous stroma can be recognized by comparison of the figures representing the various stromatic types, and the descriptions of the species studied, in this paper. Inferences or conclusions based on form or structure might seem to be misleading but it is believed from a close study of the fungi involved in this paper that the developmental stages of these forms are as given in the following paragraphs.

The simplest forms, perhaps the most primitive, because of the slight adaptation to their hosts, are those whose stromata are entirely superficial. The stroma varies in complexity ranging from *Dothichloe atramentosa* which is made up of fine, nearly hyaline, gelatinous filaments in the center surrounded by a somewhat loose pseudoprosenchyma which is dothideaceous, to one like *Pauahia Sideroxyli* which has a quasi-dothideoid structure; and finally *Halstedia portoricensis* composed of a very dense pseudoprosenchyma.

At a little higher step in development are the fungi which appear superficial but are fastened to the host by a scant hypostroma. The simplest of these is shown in *Actinodothis Perottetiae* with an extensive epistroma of compressed pseudoparenchyma and a hypostroma consisting merely of thin, hyaline, mycelial haustoria which penetrate into the epidermis and extend for some distance into the host without branching or clumping (PLATE 3, FIG. 40). In *Palawaniella Eucleae* the epistroma is more elementary than that of *A. Perottetiae*, the loculiferous region being, for the most part, composed of paraphyses with a very slight accumulation of pseudoparenchyma at the periphery. But the hypostroma is more advanced, even though consisting of thin mycelial threads, for the penetrating threads enter certain of the epidermal cells eventually filling and packing them with a dense black stroma (Fig. 3. Bothalia **1**: 17. 1921). A slightly more advanced form is exemplified in *Polystomella costaricensis* which appears superficial but its hypostroma is somewhat more extensive, in that its dark stroma penetrates

certain of the cells of the epidermis. The interior of the epistroma is composed of thin, filamentous hyphae, but the outer part is made up of typical dothideoid stroma.

Another stage in the course of development is represented by those fungi that are subcuticular. It appears that these forms, which are entirely confined to the region between the cuticle and epidermis, represent a more advanced form than those that are largely superficial with a more or less developed hypostroma. *Phaeodothopsis Eupatori* has a well developed subcuticular loculiferous region composed of compressed, linear pseudoprosenchyma while *Anisochora Tabebuiae* (PLATE 1, FIG. 25), *Euryachora betulina* and *Euryachora sp. indet.* are of practically the same complexity, being made up of dothideoid stroma, the former having a somewhat lighter appearance, but none of the four give any evidence of a hypostroma. *Aulacostroma palawanense* (Fig. 7. Phil. Jour. Sci. **9**: 177. 1914) is a bit higher in that it has a scant hypostroma in the epidermal cells although the greater part of the loculiferous region is composed of paraphyses.

The fungi which are located in the epidermis represent a still more highly developed stage. In those forms which are epidermal *Catacaumella Gouaniae* is the only one studied that gives no evidence of a hypostroma. Here the endostroma is a well developed dothideoid structure. Of the other three *Trabutia Xylosmae* possesses a pseudoprosenchymatous structure, the hypostroma occurring between the host cells; *Catacauma Zanthoxylonis* is partially dothideoid and the hypostroma is both between and within the cells of the host; while *Phaeochora Neowashingtoniae* is dothideaceous and the hypostroma is within the host cells.

Fungi below the epidermis represent a still greater adaptation. Of those *Phragmocauma viventis*, although being dothideoid, has no visible hypostroma and ranks as the simplest of this group. *Diplochorella amphimelaena* is composed of pseudoprosenchyma and has a hypostroma made up of bead-like mycelium that penetrates between the cells of the host tissue. *Phaeochorella Parinarii* has a dothideoid epistroma and a hypostroma composed of light-colored, somewhat delicate mycelium. *Catacauma Ocoteae* has a dark grey pseudoprosenchyma, with a well de-

veloped intercellular hypostroma; *C. palmicola* is composed of compressed, elliptical to linear pseudoprosenchyma; while *Uleodothis Pteridis* has a dothideoid structure. The hypostroma of both occurs within the host cells. *Scirrhia rimosa* has a dothideoid epistroma and a hypostroma of much compressed pseudoprosenchyma which gives it the appearance of blocks of stromatic tissue.

A still higher development is seen in the erumpent-superficial types. *Systremma Pterocarpi* with its epistroma and the lack of a definite hypostroma occupies the lowest position. *Dothidina disciformis* is slightly more advanced because of its dothideoid epistroma (PLATE 2, FIG. 32). *Achorella costaricensis* because of its dothideoid, intercellular hypostroma and an epistroma of pseudoprosenchyma comes next. Of the six which have their hypostroma both within and between the host cells *Montagnella maxima* has an epistroma of pseudoprosenchyma and *Achorella guianensis* has an epistroma with a quasi-dothideoid structure. *Nowellia guianensis* and *Yoshinagella polymorpha* stand out from the rest because of the dothideoid central foot. *Coccostromopsis palmigena* and *Dothidella Parryii* possess dothideaceous epistromata and a pseudoprosenchymatous central foot. In the group which has the hypostroma occurring within the host cells *Dothidina costaricensis* stands first in simplicity in that it has no central foot; the epistroma is composed of pseudoprosenchyma with a tendency toward a dothideoid structure. *Achorella Attaleae*, while possessing no central foot, has a dothideaceous epistroma and is a little more advanced. *Schweinitziella palmigena* stands alone because the epistroma is composed of pseudoparenchyma surrounding loosely tangled, hyphal filaments and with a central foot that has a false palisade structure. *Bagnisiopsis peribebuyensis* is next in complexity with an epistroma of quasi-dothideoid structure and a central foot of pseudoprosenchyma. The remaining species of this group: *Apiospora carbonacea, Corynelia portoricensis, Dothidella portoricensis, Dothidina palmicola* and *Microcyclus Walsurae* fall in the same category, having a dothideoid epistroma and a central foot.

In the final and highest developmental stage occur the fungi which lie entirely within the mesophyll of the host tissue. The

genus *Phyllachora*, the largest of this group, will be considered in a separate paper later. *Haplothecium guianense* with its mesostroma composed of a loose hyphal weft marks the lowest stage. In the order of their complexity then are seen *Ophiodothella panamensis* with its nearly hyaline, thin-walled pseudoparenchyma; *Phyllachorella Schistocarphae* with a very scant pseudoparenchyma; *Dictyochorella Andropogonis* with a stroma consisting only of a locule border of pseudoparenchyma and a clypeus; *Scolecodothis Ingae* and *Endodothella Tapirae* with a scant mesostroma composed of pseudoparenchyma, the latter considerably darker than the former; *Uleodothis Paspali* with a smoky grey pseudoparenchyma; *Dothidea tetraspora* with a characteristic pseudoparenchymatous mesostroma; *Oligostroma Suttoniae* with a scant mesostroma of pseudoprosenchyma; and *Sphaerodothis sphaerosperma* with a mesostroma of pseudoprosenchyma with a tendency toward dothideoid structure. *Teratosphaeria fibrillosa* with its stroma of light colored mycelium is rather questionable from a taxonomic standpoint. This genus was first placed in the Clypeosphaeriaceae, later removed to the Dothideales by Theissen and Sydow and finally returned to the Sphaeriales. *Desmotascus portoricensis* has both the characters of the Dothideales and the Sphaeriales in that the locules or perithecia are sphaeriaceous when solitary and resemble dothideoid structure when two or three are together. *Dibotryon morbosum* with an endostroma of pseudoprosenchyma and a hypostroma composed of bundles of mycelium between the host cells represents a high stage of development according to Theissen and Sydow because of perithecia and pseudoparenchyma between the asci. *Anthostomella Rhizomorphae* and *A. Rhizophorae* have a definite perithecial wall and a clypeus and belong to the Sphaeriales. *Stegastroma guianensis* falls in the same category and differs from the two mentioned only in the thickness of the clypeus. *Dothidella ribesia* stands out from the rest in that it occurs in the cork tissue of stems and is made up of a characteristic pseudoparenchyma (PLATE 2, FIG. 34).

The Dothideales are, by Theissen and Sydow, set apart from all the other orders by the absence of a perithecial wall and the lack of a definite ostiole. From the lack of a definite perithecium

in the Dothideales it naturally follows that the ostiole, formed by the continuation of the perithecial wall, is absent. Since there is no ostiole the fungi can discharge their spores only by means of some kind of rupture in the stroma above the locules. Some fungi, more especially of the genus *Phyllachora*, showed an ostiolate tendency but in no case was any trace of periphyses noticed as is described for *Phyllachora graminis* by Orton (**13**).

The genus *Dothidea* was erected by Fries (**7**) and later Fuckel (**8**) erected the family Dothideaceae with *Dothidea* as the type genus. In 1897 Lindau (**12**) erected the order Dothideales with a single family, Dothideaceae. Theissen and Sydow in their monographic work on the order made the distinguishing feature of the Dothideaceae the parallel, pseudoprosenchymatous structure of the hyphae. The Polystomellaceae was erected by them as a family of the Dothideales but later it was removed to the Hemisphaeriales because of the radiate form of the fruiting stroma. However, in the present study of *Polystomella costaricensis* the stroma is seen to be composed of dark, linear pseudoprosenchyma which is typically dothideaceous surrounding loosely tangled, hyphal filaments. This fungus therefore appears to represent a border line form between the Hemisphaeriales and Dothideales.

That typical dothideoid stroma is not always confined to the Dothideales is shown in *Dothichloe atramentosa* and *Corynelia portoricensis*. The genus of the first of these was erected by Atkinson (**1**, **2**) to include the species of *Hypocrella* possessing a dothideaceous stroma. The center of the loculiferous region takes on a filamentous, gelatinous appearance but the outside is composed of stroma that is dothideoid in character. Chardon (**5**) examined a set of prepared slides made from the type specimen of *Hypocrea atramentosa* and states that the stroma is dothideaceous, and there is no perithecial wall present, but that in the possession of filiform spores and other minor characters it resembles the Hypocreales. He fails to mention what the "minor characters" are, but the presence of filiform spores should not remove this genus from the Dothideales since several genera in that order possess spores of like nature.

The family Coryneliaceae was erected by Saccardo (**16**) in 1891 to include the genera *Corynelia* and *Tripospora*. Lindau

(**12**) in his work on the Sphaeriales includes the family in that order. Both of these authors describe the perithecium of *Corynelia* as ostiolate and therefore typical of the Sphaeriales. In my own observations on *Corynelia portoricensis* I failed to see a definite ostiole but attributed this to the fact that the material was too young. However, a definite neck or rostrum develops about the top of the perithecium (PLATE 3, FIG. 42). Fitzpatrick (**6**) states that his observations have shown that the family lacks the typical ostiole of the Sphaeriales but does possess a mouth or irregularly split opening. He says that the erumpent stroma and the absence of superficial mycelium makes the family unlike the Perisporiales, and the absence of a typical ostiole excludes it from the Sphaeriales. They resemble the Perisporiales more than Sphaeriales in his opinion and he suggests their incorporation in the former order after the limits have been expanded somewhat. However, in the study of this fungus from microtome sections the stroma was found to be typically dothideaceous (PLATE 3, FIG. 42), and fastened to the host by a wide central foot. It might appear as a transition from between the Perisporiales and Dothideales.

There are some fungi which appear to mark a connecting link between the two orders just mentioned. In *Achorella Attaleae* we find that the locules are borne as perithecium-like protuberances on the stroma and that there is a superficial mycelium present. This fungus possessing characters of both orders has an epistroma typically dothideaceous in structure and although showing closest connection with the Dothideales presents a transition form between it and the Perisporiales.

In the key of Theissen and Sydow they emphasize the absence of setae in the genus *Yoshinagella*. However, *Yoshinagella polymorpha* agrees in all particulars with the characters of the genus with the exception of the setae. The presence or absence of setae do not seem to be good characteristics in setting apart a genus and Stevens (**20**) suggests broadening the conception of the genus *Yoshinagella* and admitting forms with stromatic setae. Comparison of *Y. polymorpha* with specimens of *Asterina comata*, the type species of the genus *Trichodothis*, shows that the stromata and setae are similar and that they are separated only by spore

characters. It appears therefore that stroma rather than setae should be the deciding factor.

The family Pseudosphaeriaceae was erected by von Höhnel (**10**) to include the two genera *Wettsteinina* and *Pseudosphaeria* and later he added many more genera. The family was characterized by the presence of pseudoparenchyma between the asci and monoascicular locules. Concerning this von Höhnel states that it is a noteworthy connecting link between the Dothideales and the Sphaeriales. In their monographic work on the Dothideales Theissen and Sydow, in a supplement, have spoken of the Pseudosphaeriaceae and assigned to it several genera which von Höhnel had considered as dothideaceous. They divided the family into three groups, namely: Botryosphaeriaceae, Pyrenophoreae, and Dothioreae, and considered it as a highly developed form of the Myriangiales. Later the same authors (**18**) raised the family to the rank of an order. In the outline of the Pseudosphaeriales Theissen and Sydow state that almost all the forms which they described as belonging to the Dothideaceae possessed an interascicular pseudoparenchyma. In the present study five fungi, namely *Scirrhia rimosa*, *Dibotryon morbosum*, *Desmotascus portoricensis*, *Montagnella maxima*, and *Dothidella Parryi*, possessed this interascicular pseudoparenchyma. Of this number *Dibotryon* was the only genus to be included in the order Pseudosphaeriales. *Desmotascus portoricensis* has been considered by Stevens (**19**) as belonging to the Sphaeriales. *Scirrhia rimosa* belongs to the Phyllachoraceae, *Montagnella maxima* to the Montagnellaceae, and *Dothidella Parryii* to the Dothideaceae.

In the present discussion the fungi are classed as to complexity of their structure but it does not follow that this is representative of their phylogeny. In the grouping in this article the succession of forms is as follows: (1) entirely superficial; (2) superficial with haustoria; (3) superficial with a scant hypostroma; (4) superficial with a rather well developed hypostroma; (5) subcuticular with no evidence of a hypostroma; (6) subcuticular with a hypostroma that is scant or well developed; (7) epidermal with no evidence of a hypostroma; (8) epidermal with a hypostroma scantily or well developed; (9) subepidermal with a hypostroma scantily or

well developed; (10) erumpent-superficial with or without a definite foot; and finally (11) those which are entirely imbedded within the host tissue. In the order of their complexity as to stromata structure are seen (1) pseudoparenchyma, (2) pseudoprosenchyma, and (3) dothideoid structure. Those fungi with the stroma between the cells of the host have been considered as the most primitive and in order of their complexity are those which are both between and within the host cells, and finally those which are entirely within the cells of the host tissue. The Sphaeriales, because of a definite perithecial wall and ostiole, have been considered higher than the Dothideales, while the Pseudosphaeriales appear to represent an intermediate form between the two orders.

SUMMARY

1. Forty-six genera with 85 species of fungi were examined and compared as to their stromata and to their relation to their hosts. They were mainly of the Dothideales but other orders and families showing related structures were included for comparison.

2. In order to designate the various structures of the morphological units involved in this study some new terms have been coined and they are as follows: border, extraloculiferous stroma, foot, interlocular region, lining, loculiferous region, mesostroma, and plug.

3. In studying the structure of the fungi the most salient factors, which serve as distinguishing morphological characters, have been noted.

4. The stromata studied are composed of one or more of three fundamental parts, namely: (1) loculiferous region; (2) extraloculiferous stroma; and (3) hypostroma.

5. The loculiferous region varies in complexity from a slight accumulation of pseudo-tissue, around, above, or below the border of the locule, to a large complex stroma, in which several to many locules are borne. It may consist of either endostroma or epistroma.

6. In certain of the fungi the locules are surrounded by a more or less dense layer of stroma, the border.

7. Some of the fungi possess a rind composed of dense black stroma two or three cells in thickness.

8. No definite ostiole has been found in the study of the fungi involved in this paper except those which obviously belong to the Sphaeriales.

9. Extraloculiferous stromata are found in only a few fungi, the greater number of these belonging to the Phyllachorineae. They usually consist of two parts, the rind and mesostroma.

10. The hypostroma appears in many different forms. It occurs as follows: (1) as very thin, mycelial threads which penetrate the epidermis and extend as haustoria into the host tissue without branching or clumping; (2) as thin mycelial threads penetrating the host and filling certain of the epidermal cells with dark masses of mycelium; (3) as loose intercellular mycelium; (4) as more or less compact masses of mycelium within the host cells; (5) as subcuticular or subepidermal sheet-like masses of stroma; (6) as a column-like or knobby protruding foot; and (7) as various combinations of these forms.

11. In recording the location of stromata upon or within the host tissue the following types have been recognized: (1) superficial; (2) subcuticular; (3) epidermal; (4) subepidermal; (5) erumpent-superficial; and (6) lying within the mesophyll.

12. The loculiferous region is composed of pseudoparenchyma or pseudoprosenchyma of varying density. The cells of the pseudoparenchyma are approximately isodiametrical while those of the pseudoprosenchyma are palisade-like, ellipsoid in form, or long, parallel walled.

13. Nearly all of the fungi examined possessed a concentric layer of thin, hyaline, compressed cells around the periphery of the locule, the lining.

14. Each species of fungus has been classed as to the stroma type to which it belongs and as to the complexity of its structure. With respect to the complexity of structure they have been arranged as to location, density of the epistroma or endostroma, and the position the hypostroma occupies in the host tissue. Those fungi which are entirely superficial have been considered the most primitive, with those that are subcuticular, epidermal, subepidermal, erumpent-superficial, and lying within the meso-

phyll varying in complexity in the order named. Those whose stromata are composed of pseudoparenchyma have been regarded as the simplest types while those made up of pseudoprosenchyma in its various forms have been considered as more highly developed. In the order of its complexity the hypostroma occurs between the cells, both within and between the cells, and finally within the cells of the host tissue.

15. The presence of dothideoid stroma is not confined to the order Dothideales but is found in *Corynelia portoricensis*, which possibly belongs to the Perisporiales, and *Dothichloe atramentosa*, which is in the Hypocreales.

16. Fungi possessing an interascicular pseudoparenchyma, the distinguishing feature of the Pseudosphaeriales, are found in the Dothideales and Sphaeriales.

17. In *Polystomella costaricensis* and *Dothichloe atramentosa* the stroma is composed of loosely tangled, hyphal filaments surrounded by a dothideoid structure. Inasmuch as there is such variation in the same fungus this character is not of high morphological value.

18. *Yoshinagella* is set apart from *Trichodothis* by spore character and lack of stromatic setae. However, since these setae fluctuate considerably in very closely related species of the same genus it seems proper to consider stroma rather than setae as the distinguishing characteristic of a fungus.

ACKNOWLEDGMENT

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ALABAMA POLYTECHNIC INSTITUTE,
AUBURN, ALABAMA

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EXPLANATION OF PLATES

PLATE I

Fig. 24. Photomicrograph of *Scirrhia rimosa* showing complex stroma with many locules and a hypostroma in blocky formation.

Fig. 25. Photomicrograph of *Anisochora Tabebuiae* showing light colored, thin-walled, dothideoid stroma, and an extraloculiferous stroma.

Fig. 26. Photomicrograph of *Nowellia guianensis* showing a hypostroma, with foot, below a superficial epistroma.

Fig. 27. Photomicrograph of *Phyllachora Phaseoli* showing a very simple stroma and a clypeus just covering the top of the locule.

Fig. 28. Drawing of a locule showing the lining.

Fig. 29. Drawing of a locule showing an ordinary hymenium.

Fig. 30. Photomicrograph of *Dothidea tetraspora* showing a locule with a mammiliform hymenium.

PLATE II

Fig. 31. Locule of *Scirrhia rimosa* showing interascicular pseudoparenchyma and plug.

Fig. 32. Photomicrograph of *Dothidina disciformis* showing rind extending entirely around the loculiferous region.

Fig. 33. Drawing showing typical dothideoid stroma.

Fig. 34. Photomicrograph of *Dothidella ribesia* showing hypostroma made up of a close weft.

Fig. 35. Drawing of *Phyllachora Engleri* showing endostroma of loose weft.

Fig. 36. Drawing showing irregular pseudoparenchyma.

PLATE III

Fig. 37. Drawing of *Polystomella costaricensis* showing loosely tangled, gelatinous, hyphal filaments surrounded by dothideoid stroma.

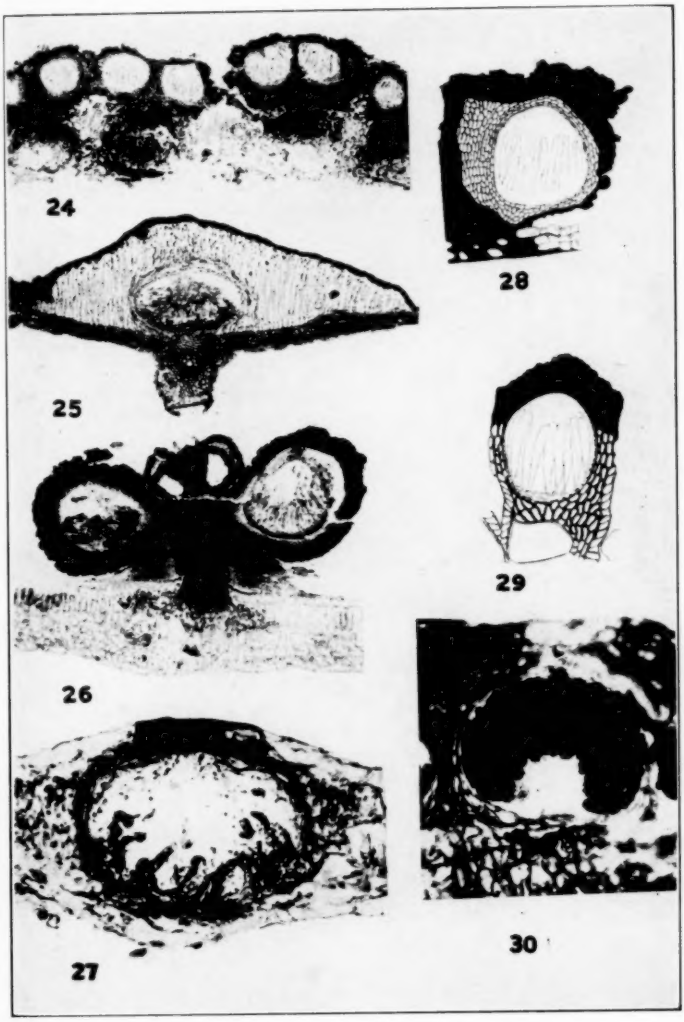
Fig. 38. Drawing of *Phyllachora Trophis* showing imperfect clypei.

Fig. 39. Photomicrograph of *Phyllachora Engleri* showing dense locule border and clypei greatly exceeding the loculiferous region.

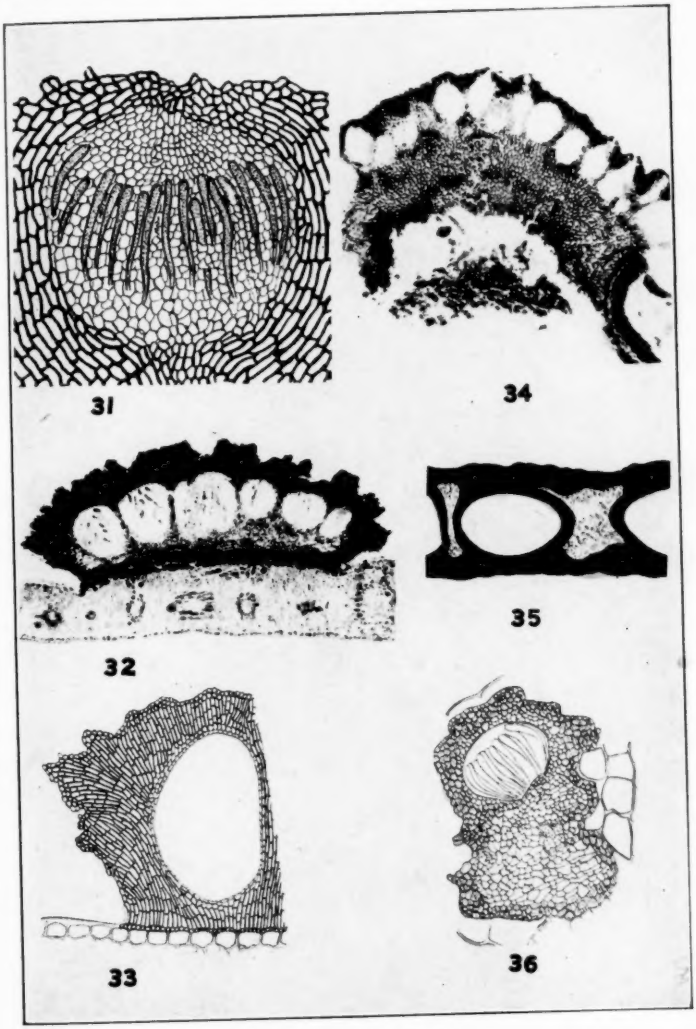
Fig. 40. Drawing of *Actinodothis Perottetiae* showing haustoria penetrating the host tissue.

Fig. 41. Drawing of *Dothidina costaricensis* showing ellipsoidal pseudoprosenchyma.

Fig. 42. Drawing of *Corynelia portoricensis* showing neck of perithecium and dothideoid stroma.



MORPHOLOGY OF STROMATA



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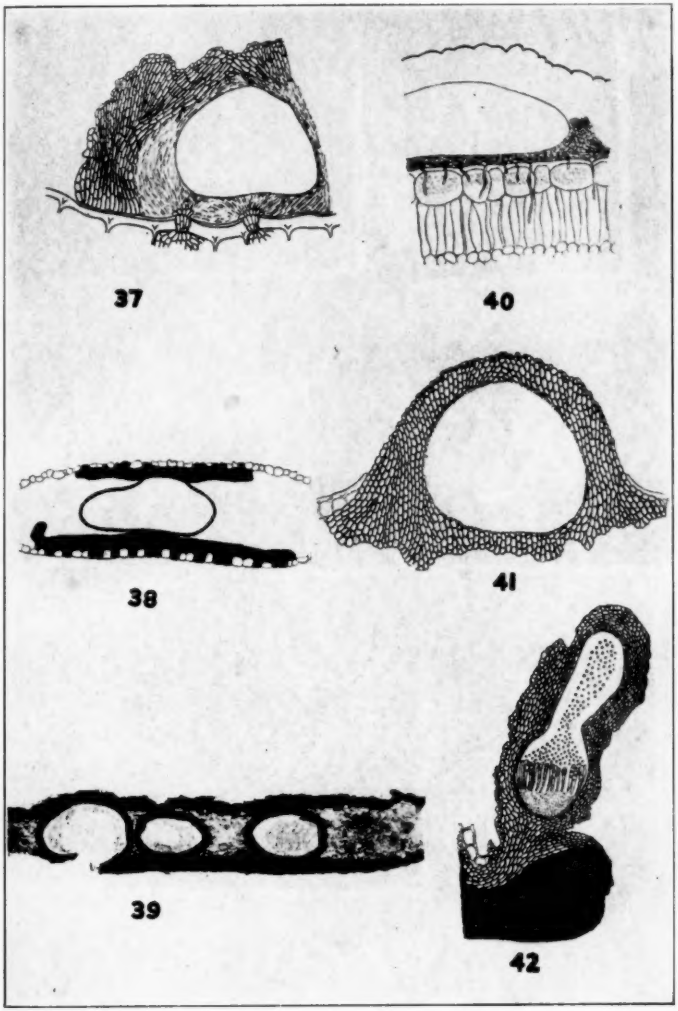

MORPHOLOGY OF STROMATA

FURTHER EVIDENCE OF PHYSIOLOGIC RACES OF OAT SMUTS[1]

GEORGE M. REED

In a previous publication (**2**), I have described the occurrence of physiologic races in both the loose (*Ustilago Avenae* (Pers.) Jens.) and covered (*U. levis* (Kellerm. & Swingle) Magn.) smuts of oats. The facts reported were based on experiments with two collections of each species. One collection of each smut was originally obtained in Missouri and had been used in various experiments during a period of several years. The other two collections were obtained from the Welsh Plant Breeding Station, Aberystwyth, Wales, through the courtesy of Director R. G. Stapledon and Miss Kathleen Sampson. The results of the series of experiments with these four collections gave clear evidence of the existence of specialized races in both species of smut.

The two races of loose smut were characterized by their ability to infect a large number of varieties of oats which were grown in the experiments. The most obvious difference between them was the failure of the race from Wales to cause a severe infection of *Avena nuda* L. var. *inermis*, a variety which has proved to be highly susceptible to the Missouri race. The differences between the two races of covered smut were much more striking. The race from Missouri gave high percentages of infection on a large number of varieties, including *Avena nuda* L. var. *inermis*, *A. sativa* L. var. Canadian, Irish Tan, Monarch, Potato and Victor, *A. orientalis* Schreb. var. Black Tartar and varieties belonging to three sub-species of *A. strigosa* Schreb. These results were quite in harmony with those previously recorded for this covered smut. In contrast, the covered smut from Wales failed to infect any of the varieties of *Avena nuda*, *A. sativa* or *A. orientalis*, which were used in the experiments. In a field test with Victor some infected plants were observed. In view of later results it is probable that the seed of this variety

[1] Brooklyn Botanic Garden Contributions No. 48.

had been accidentally contaminated with some other smut. The Welsh covered smut, however, proved capable of severely infecting cultivated varieties of three sub-species of *A. strigosa*. Perhaps its most outstanding feature was its ability to infect 100 per cent of the plants of *Avena brevis* Roth., a species which had proved entirely resistant to loose smut and only occasionally had given infected plants with the Missouri race of covered smut.

Miss Sampson (**5**) has recently described some of her experiments with collections of both loose and covered smut from Wales, as well as with material from my collections. In the main her results correspond very closely with mine and the evidence, therefore, is quite conclusive that physiologic host specialization in both species of oat smuts exists.

Additional investigations have been carried out with a large number of collections of both *Ustilago Avenae* and *U. levis* which have been obtained from many sources. As yet it has been possible to test these on only a few varieties of oats. So far as determined most of the collections of smut do not appear to show any marked differences from the Missouri races. It is possible that if the investigations were carried further, involving the use of a wider range of oat varieties, distinctions between some of them might be evident. A few new races, however, of both loose and covered smut have been isolated and some of these are of special interest.

Some of the experiments have been carried out in the greenhouse where specially favorable conditions for infection were available (**3**). In these tests the usual method was to germinate the inoculated seed in moderately dry sand at a constant temperature of 20° C. After germination the seedlings were transferred to the benches where the plants grew to maturity. In the field experiments, the inoculated seed was sown directly in the ground and, as might be expected, the percentage of infection was usually not as high as in the greenhouse cultures.

PHYSIOLOGIC RACES OF USTILAGO AVENAE ON FULGHUM AND RED RUSTPROOF OATS.—In previous studies (**1**, **4**) on the behavior of oat varieties towards the oat smuts, it was found that strains of Fulghum and Red Rustproof consistently proved to be very highly resistant. Several strains of each variety have

been obtained from different sources and they have all shown a similar behavior. Usually no infection was obtained, although occasionally a small percentage of smutted plants was observed. The strains of both varieties have clearly shown a high degree of resistance in previous experiments.

Fulghum and Red Rustproof oats are grown extensively in the southern United States where they are usually sown in the fall. In recent years, selections from them have proved successful in the southern part of the spring oat section. Although these varieties have shown a high degree of resistance to the smuts in our previous experiments, yet it is an interesting fact that in the southern states where they are extensively grown, the occurrence of oat smut in considerable quantities has been reported. It is possible, of course, that much of the smut observed has been on the Winter Turf varieties which are also grown throughout the southern oat section.

With the discovery of specialized races of oat smuts, an effort was made to secure collections of smut from various southern localities with a view to determining whether there are races especially adapted to attacking the Fulghum and Red Rustproof varieties. The quest has been particularly successful, as several collections have been secured which are capable of producing a high degree of infection in one or other of these varieties. The results with these collections are given in TABLE I.[2]

Three collections have shown a marked capacity for infecting the strains of the variety Fulghum. Collection No. 1 was obtained from Dr. L. R. Hesler of the University of Tennessee, Knoxville, Tenn. The material was received in the summer of 1924 and four experiments were carried out, two in the greenhouse and two in the field in 1925 and 1926. Collection No. 2 was received from Mr. T. R. Stanton, Office of Cereal Investigations, United States Department of Agriculture. The smut was obtained on Fulghum at Lawton, Oklahoma, in June, 1925, and was used in two series of experiments—one in the greenhouse and the other in the field. Collection No. 3 was obtained from Mr.

[2] It must be emphasized that the statements made regarding the behavior of the varieties apply only to the strains used and numbered in the tables. Other strains of varieties may show a different behavior.

P. B. Dunkle, Superintendent, Sub-Station No. 6, Texas Agricultural Experiment Station, Denton, Texas. The smut was collected on the variety Fulghum in June, 1925, and has also been used in two experiments, one under greenhouse conditions and the other in the field.

TABLE I

PHYSIOLOGIC RACES OF USTILAGO AVENAE ON FULGHUM AND RED RUSTPROOF

Species and variety	Seed No.	Fulghum race									Red Rust-proof race		
		Collection No. 1			Collection No. 2			Collection No. 3					
		No. pl.	No. inf.	% inf.	No. pl.	No. inf.	% inf.	No. pl.	No. inf.	% inf.	No. pl.	No. inf.	% inf.
Avena nuda L.													
v. *inermis*	30	86	76	88.3	57	38	66.6	77	62	80.5	25	0	0
Avena sativa L.													
v. Black Diamond	116	61	29	47.5	44	37	84.0	85	65	76.4	26	1	3.8
" Black Mesdag	70	41	0	0	25	0	0	33	0	0			
" Canadian	119	39	39	100.0	24	24	100.0	24	24	100.0			
" Early Champion	197	80	35	43.7	37	36	97.2	59	55	93.2	21	1	4.7
" Early Gothland	152	73	1	1.3	53	25	47.1	78	29	37.1	29	0	0
" Monarch	161	96	21	21.8	46	19	41.3	79	14	17.8	28	0	0
" Markton	752	21	1	4.7	26	0	0	24	0	0	24	0	0
Avena sterilis L.													
v. Burt	175	50	1	2.0	20	1	5.0	23	0	0			
" Fulghum	129	82	44	53.6	49	30	61.2	77	42	54.5	25	0	0
" "	257	76	73	96.0	47	46	97.8	75	72	96.0	26	0	0
" "	264	51	45	88.2	23	22	95.6	24	22	91.6			
" "	367	29	23	79.3	25	18	72.0	30	23	76.6	28	0	0
" "	696	71	49	69.1	25	23	92.0	26	24	92.3			
" "	745	55	46	83.6	57	41	71.9	73	41	56.1	30	1	3.3
" Red Rustproof	131	69	0	0	54	0	0	80	0	0	27	8	29.6
" " "	262	22	0	0	22	0	0	27	0	0	27	7	25.9
" " "	263	25	0	0	28	0	0	51	0	0	29	19	65.5
" " "	265	76	0	0	55	2	3.6	82	2	2.4	24	17	70.8
" " "	355	52	0	0	29	0	0	27	0	0			
" " "	746	53	0	0	29	0	0	68	0	0	29	18	62.0

These three collections have shown remarkable uniformity in their capacity for infecting the oat varieties tested. Six different strains of Fulghum have been used in the experiments and all have proved to be severely infected, the percentage of infection varying from 53.6 to 97.8 per cent. In individual tests with some strains all of the inoculated plants were smutted. Fulghum No. 129 has consistently proved to be somewhat less susceptible than the other strains.

In contrast to the severe infection of Fulghum the strains of Red Rustproof gave negative results. Six strains were grown

in the experiments and only four infected plants were observed in one of them. The variety Burt also proved to be very resistant.

All three of these collections have severely infected *Avena nuda* L. var. *inermis*, *A. sativa* L. var. Black Diamond, Canadian and Early Champion, while Early Gothland, a variety very susceptible to the Missouri race of loose smut, has proved to be only moderately infected and Monarch, a variety very resistant to the Missouri race, has shown a fair degree of susceptibility to all three collections. Black Mesdag consistently remained free from infection and only one doubtful plant of Markton was smutted.

A collection of *Ustilago Avenae* on Red Rustproof oats was also received from Superintendent Dunkle in June, 1925. An experiment in which several varieties were inoculated with these spores was carried out in the greenhouse. Five strains of Fulghum were used and a percentage of infection of 13.7 to 100 was secured. Five strains of Red Rustproof were also used and 30.4 to 55.8 per cent were infected. In view of the fact that this collection of smut gave infection on strains of both Fulghum and Red Rustproof, while the other collection from Mr. Dunkle on Fulghum did not infect Red Rustproof, it was thought possible that the original material may have contained a mixture of smut from the two varieties of oats. Accordingly, spores were carefully collected on both Red Rustproof and Fulghum from this greenhouse experiment and used in a field test, the results of which are given in TABLE I. It is clear from the data obtained that the spores collected on Red Rustproof are incapable of infecting strains of Fulghum, while at the same time causing a more or less severe infection of strains of Red Rustproof. It was further found that the spores collected in the greenhouse on Fulghum produced a severe infection of Fulghum but not of Red Rustproof. The evidence seems clear that the original collection contained a mixture of smutted heads of Fulghum and Red Rustproof.

The data clearly indicate that distinct races of *Ustilago Avenae* attack Fulghum and Red Rustproof oats. The Fulghum race is characterized by its ability to severely infect several

strains of Fulghum and also *Avena nuda* var. *inermis*, *A. sativa* var. Black Diamond, Canadian, Early Champion and moderately Early Gothland and Monarch. Some varieties, as Black Mesdag, Markton, Burt and Red Rustproof, remain free from infection, or practically so. The Red Rustproof race, on the other hand, seems to be confined to the strains of this variety, practically negative results being obtained on all the other varieties grown in the experiment.

COMPARISON OF USTILAGO AVENAE AND USTILAGO LEVIS FROM MISSOURI.—In previous publications (**1**, **4**) the general similarity in the capacity for infecting oat varieties by the Missouri races of these two smuts has been emphasized. Most cultivated varieties of oats are susceptible to both species and, as a rule, if a variety is susceptible to one species, it is susceptible to the other, and if it is resistant to one, it is resistant to the other. However, several varieties of oats seem to be more susceptible to the loose smut than to the covered, while a very few varieties have behaved in the opposite manner. It has been possible to secure additional data on the behavior of these varieties along with a few which are either highly susceptible or highly resistant to both. The data are presented in TABLE II.

In line with the studies previously reported, such varieties as *Avena nuda*, *A. sativa* var. Canadian, Early Champion and Victor, and most of the varieties of *A. strigosa* proved to be equally susceptible to both races, usually giving practically 100 per cent infection. Black Mesdag, Joanette, Burt, Fulghum and Red Rustproof and one variety of *Avena strigosa* have proved to be extremely resistant to both smuts. There is, however, a group of varieties of *Avena sativa*, including Black Diamond, Black Norway, C. I. 602, Danish, Danish Island, Early Gothland, Green Russian, Irish Victor, Japan, Monarch Selection, Nebraska No. 21, Rossman, Scottish Chief, Trisperma and White Queen, which are susceptible to *Ustilago Avenae*, while giving either negative results or low percentages of infection with *U. levis*. One variety of the side oat group has given a similar result. On the other hand, Monarch has proved to be very susceptible to *U. levis*, while manifesting a high degree of resistance to the Missouri race of loose smut.

TABLE II

COMPARISON OF MISSOURI RACES OF USTILAGO AVENAE AND USTILAGO LEVIS

Species and variety	Seed No.	*Ustilago Avenae*			*Ustilago levis*		
		Total plants	No. inf.	Per cent inf.	Total plants	No. inf.	Per cent inf.
Avena barbata Brot.	830	23	23	100.0	26	26	100.0
Avena brevis Roth.	289	51	0	0	58	3	5.1
Avena nuda L. var. *inermis*	30	74	71	95.9	60	57	95.0
Avena sativa L.							
v. Black Diamond	116	34	32	94.1	37	4	10.8
" Black Mesdag	70	42	0	0	42	0	0
" Black Norway	118	33	18	54.5	38	0	0
" Canadian	119	56	55	98.2	53	53	100.0
" C. I. 602	145	49	49	100.0	52	8	15.3
" Danish	309	50	50	100.0	57	0	0
" Danish Island	149	17	17	100.0	20	4	20.0
" Early Champion	197	20	17	85.0	24	24	100.0
" Early Gothland	152	62	60	96.7	74	2	2.7
" Green Russian	316	50	34	68.0	58	0	0
" Irish Victor	206	46	46	100.0	50	2	4.0
" Japan	207	85	52	61.1	67	3	4.4
" Joanette	187	47	0	0	53	0	0
" Monarch	161	67	1	1.4	64	63	98.4
" Monarch Selection	162	40	39	97.5	47	0	0
" Nebraska No. 21	280	25	21	84.0	20	0	0
" Rossman	322	47	46	97.8	50	0	0
" Scottish Chief	124	53	20	37.7	59	0	0
" Trisperma	64	40	40	100.0	48	0	0
" Victor	126	32	32	100.0	57	57	100.0
" White Queen	327	36	36	100.0	47	3	6.3
Avena orientalis Schreb.	246	64	62	96.8	69	1	1.4
Avena sterilis L.							
v. Burt	175	10	0	0	15	0	0
" Fulghum	129	49	3	6.1	47	3	6.3
" Red Rustproof	131	39	0	0	41	2	4.8
Avena strigosa Schreb.							
sub-sp. *glabrescens albida*	587	47	19	40.4	45	38	84.4
" " *cambrica*	588	29	0	0	21	0	0
" *orcadensis flava*	589	30	30	100.0	19	19	100.0
" " *intermedia*	590	25	24	96.0	18	17	94.4
" *pilosa fusca*	593	29	26	89.6	21	19	90.4

Occasionally plants of one strain of *Avena brevis* Roth. infected with covered smut were also obtained, although no infection of the species by the loose smut has occurred. *Avena barbata* Brot. has proved to be very susceptible to both smuts.

These results confirm the earlier data as to the behavior of these two smuts on the varieties grown. Although both are capable of attacking a large number of varieties belonging to the different species of oats yet they can be differentiated by differences in their capacity for infecting certain varieties.

BROOKLYN BOTANIC GARDEN,
BROOKLYN, N. Y.

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SCOLECOBASIDIUM, A NEW GENUS OF SOIL FUNGI

E. V. Abbott

(With Plate 4 and 1 Text Figure)

While making a study of the fungous flora of Louisiana soils, two fungi were isolated quite commonly which did not seem to belong to any genus of fungi now described. On the medium used for isolating fungi from the soil, an acidified synthetic agar, these organisms appeared as small brownish to black colonies, at first almost entirely submerged, but later developing aerial mycelium and producing conidia. They were isolated from both cotton and sugar cane soils.

The distinguishing characters of these fungi are the shape of the conidia and the method of bearing the conidia on the conidiophores. The conidia of one species, *Scolecobasidium terreum* (Text Fig. 1-*a*; Plate 4-*A*), are T- or Y-shaped, while those of *S. constrictum* (Text Fig. 1-*b*; Plate 4-*B*) are oblong with a constriction in the center. The conidia of both are two celled and lightly olivaceous.

The type of conidia production is the same in both species (Text Fig. 1-*a*, *c*). From the ends of the short conidiophores one, two, or three short, thread-like sterigmata arise, each of which bears a terminal conidium. The thread-like nature of the basidia or sterigmata suggested the term *Scolecobasidium* as a generic name.

When the classification of these fungi was first being considered, there was some question as to whether both could be classified properly in the same genus in view of the shape of the conidia. *Scolecobasidium terreum*, which has T- or Y-shaped conidia, might be considered as belonging to the Dematiaceae-Staurosporeae, while the shape of the conidia of *S. constrictum* places it in the Dematiaceae-Didymosporeae. However, the type of fructification and of conidia germination, which are identical in the two (Text Fig. 1-*b*, *d*), and the similarity in the colony

characteristics of the two organisms, show them to be at least very closely related forms. Since the point in question is largely a matter of opinion, they were classified in a single genus, which the author would place with the Dematiaceae-Didymosporeae.

Scolecobasidium gen. nov.

Hyphae creeping, septate; conidiophores arising as short side branches from aerial hyphae, not erect, non-septate. Conidia elongate, two celled, smooth, light olivaceous to almost hyaline, borne singly on short, terminal, thread-like sterigmata; one to three sterigmata on each conidiophore.

Type species: *Scolecobasidium terreum.*

1. **Scolecobasidium terreum** sp. nov.

Cultivated on dextrose bean agar, colonies round, 2–3 cm. in diameter; surface velvety, olivaceous; reverse greenish black. Hyphae light olivaceous, septate. Conidiophores 5.0 to 8.0 μ

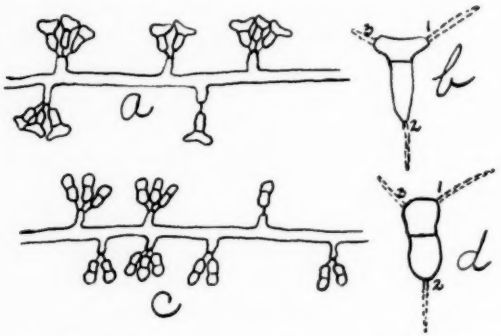


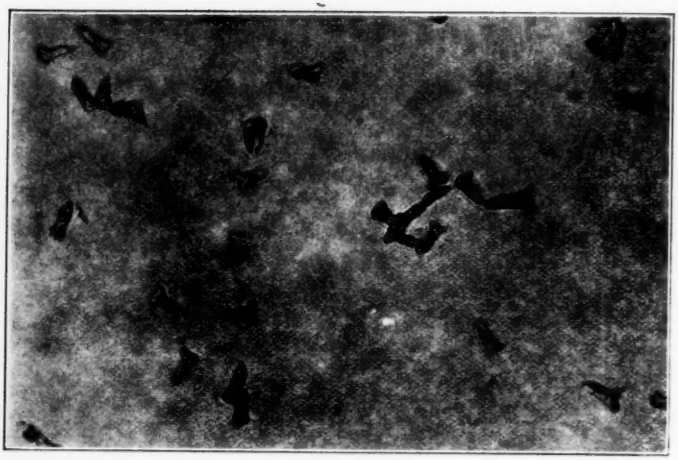
FIG. 1. *a, b-Scolecobasidium terreum, a,* conidiophores; *b,* germination; *c, d-Scolecobasidium constrictum, c,* conidiophores; *d,* germination. 1–3. germ tubes.

long by 2.0 to 2.5 μ wide. Sterigmata 0.5 to 1.0 μ long. Conidia T- or Y-shaped, two celled, light olivaceous to almost hyaline, smooth, 4.0 to 12.0 μ long by 2.0 to 2.5 μ wide. Perithecia or sclerotia not observed (TEXT FIG. 1-*a*; PLATE 1-*A*).

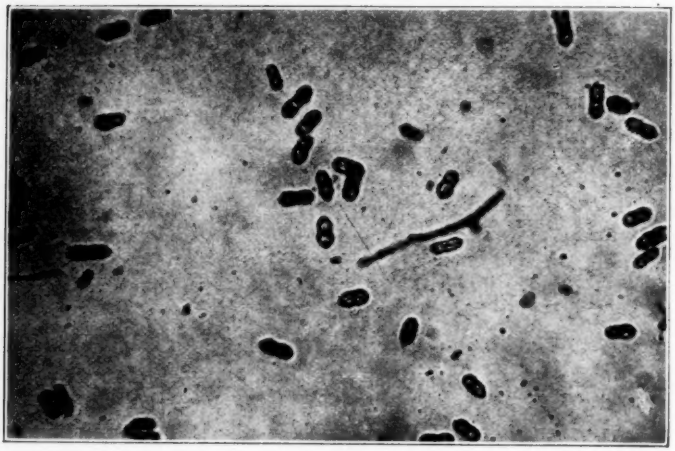
HABITAT: soil.

2. **Scolecobasidium constrictum** sp. nov.

Cultivated on dextrose bean agar, colonies round, seldom more than 3 cm. in diameter; surface fuscous, olivaceous; reverse



A



B

A. SCOLECOBASIDIUM TERREUM
B. SCOLECOBASIDIUM CONSTRICTUM

greenish black. Hyphae light olivaceous, septate. Conidiophores 5.0 to 8.0 μ long by 2.0 to 2.5 μ wide. Sterigmata 0.5 to 1.0 μ long. Conidia two celled, slightly constricted at the center, smooth, light olivaceous, 6.0 to 12.0 μ long by 2.5 to 4.0 μ wide. Perithecia or sclerotia not observed (TEXT FIG. 1-*c*; PLATE 1-*B*).

HABITAT: soil.

On Czapek's synthetic agar the growth of these fungi is slower and less abundant than on dextrose bean agar. The optimum temperature for growth is between 25° and 30° C. Slight growth occurred as high as 35° C., with no growth at 37° C.

The author is indebted to Dr. C. W. Edgerton for suggestions regarding the classification of the fungi described and for making the photomicrographs.

LOUISIANA AGRICULTURAL EXPERIMENT STATION,
BATON ROUGE, LOUISIANA

EXPLANATION OF PLATE 4

Photomicrographs of conidia of *Scolecobasidium:* A, *S. terreum* (× 825); B, *S. constrictum* (× 675).

MYXOMYCETAL MISDEMEANORS

THOMAS H. MACBRIDE

Myxomycetes are generally reckoned entirely inconsequential. Retiring in habit, obscure in structure, they are ignored by the ordinary student, and seldom collected. Apparently, innocent to a degree;—save that a single species sometimes may affect the statistics of the cabbage-field,—of service nowhere, economic importance is nil, and applied science holds them in disdain; why mention them?

But our students of practical botany are zealous people; watchful are they; on the lookout always for the welfare of field and garden, noting especially symptoms new; and, singularly enough, the slime-moulds now no longer may escape!

Recently there came to judgment from Kentucky material correctly diagnosed as representing the group in question. One specimen from a lawn or blue-grass pasture carries on the blades and stems of *Poa* typical *Physarum vernum* Somm. The other shows the starting shoots ('sets'?) of the sweet-potato, *Ipomœa*, overwhelmed apparently by a fruiting plasmodial phase of *Physarella*, doubtless *P. oblonga* (Berk. & Curt.) Morg.

This is surprising. The small *Ipomœa* must have been almost smothered, and,—if Sir Jagadis may be assumed to know anything about it at all,—at the same time nearly tickled to death! Think of a gelatinous, tortuous stream slowly creeping over every exposed, transpiring surface!

But greater was the surprise indeed when a few days later,—in fact, before the clear identification of the formless, tangled, capillitial mass that whitened the withered leaflets of the Kentucky *Ipomœa*,—a letter arrived announcing specimens from Mississippi 'under separate cover.'

Upon examination these proved to be precisely the same species on almost identical hosts, viz., on *Ipomœa* as before, and on a species of grass, *Paspalum* for *Poa*, perhaps *P. platycaule*, a valued lawn-grass in some regions.

The coincidence now becomes the thing of interest. Are we in presence of a shaping habit, or is ti some established relation until now overlooked?

So far as appears, of course, it all comes about as part of the ordinary experience of a myxomycete. Daylight the slime-mould needs not, at least for a time, if ever. For shelter and moisture it seeks the sunless regions of decay. For the *Physarum* named the rotting mat of smothered grass-leaves of turf, or lawn well-watered and enriched by constant clippings furnished ideal habitat. There the myxo may flourish all unsuspected, spreading sometimes quite equally in all directions, until maturity, when, urged perhaps by necessity for air,—the oxidation called for in spore-formation,—the plasmodium suddenly seeks the light, ascends everything climbable. Stiff, upright stems and leaves of lawn unshorn, just right, soon to be covered with hundreds of tiny sacs, each packed with uncounted, black, microscopic spores, so that when the belated gardener arrives,—perhaps in the sunny afternoon,—there rises about his flying blades sudden clouds of dust, like sooty smoke. 'Something wrong,' he's sure to say; and when, his mowing ended, he goes back to see, lo! a black shadow on his shearing, a dusky ring a yard or two in diameter, a '*fairy ring*' in fact, perhaps two or three of them; the *Physarum* has done its work. 'Smut,' the gardener says, and makes report; but the grass is none the worse,—not one whit!

The case of *Ipomœa* is much the same. Here the soil is tilled; but enriched perchance with leaf-mold, or decaying vegetable matter of some sort. On a mass of this beneath the surface, the plasmodium forms, later shaping its fruit above ground as before, on anything that there may lie. No doubt the movement (growth) of the potato-shoot greatly disturbed the easy procedure of its guest, so that not a single normal sporangium came to form!

In this case the young sweet-potato is possibly injured, growing points checked or killed; but the situation is hardly pathologic; it is the accident of one organism for the moment getting in another's way, the embarrassment apt to be mutual.

Should an entire row or field be affected, we should have occa-

sion for investigation; even that two cases should be reported, wakens desire for further information; symbiosis?

However;—misdemeanors of the sort here brought to view are not infrequent; but seldom do they provoke inquiry. A plant in bloom, two or three feet high, has been seen completely covered with the sporangia of *Physarum polycephalum; Mucilago* likes to climb the smooth stems of *Impatiens pallida* by the lake or stream; *Diachea* occasionally covers a small strawberry-patch, soiling with standing spore-case dozens of scarlet globes to the undoubted vexation of the owner. *Physarum cinereum* is also sometimes found in similar compromising situations; *Diderma simplex* on the cranberry, and various didermas and physarums affect the sedges, and crowfoots, marsh-mallows, etc., in moist ground everywhere.

But so far the misdemeanors of the myxomycete are almost negligible. Accidents they are; mere incidents in nature's wide conflict irrepressible, where every living thing is forever getting in the way of everything else that lives and grows.

IOWA CITY, IOWA

MYCETOZOA FROM PORTO RICO

ROBERT HAGELSTEIN

The following species of slime-molds were collected by the writer, while on a visit to Porto Rico, during the early months of 1926, in the company of several members of the scientific staff of the New York Botanical Garden. The greater part of the collections were made in the vicinity of San Juan, and there, at the time, the weather conditions were not favorable. The rains had ceased by December 1925, and as an interval of seven weeks of very dry weather had intervened, the fruitings in many instances were old, and much weathered, making identification difficult.

The number of species found was not large, but it is interesting to note that about one half of them were unrecorded from Porto Rico prior to this visit. It is the writer's opinion that systematic and frequent collecting by resident students who have opportunities to follow the weather's vagaries would lead to the discovery of many more species in this tropical island. It is apparent that little intensive collecting in this group has been done in Porto Rico.

The material was submitted to Dr. W. C. Sturgis, an eminent student of the Mycetozoa, for verification, and determination of obscure species and imperfect specimens. To him the thanks of the writer are due, as well as to Dr. N. L. Britton, Director of the New York Botanical Garden, Dr. B. E. Quick, of Westminster College, New Wilmington, Pa., and Mr. R. A. Toro, of the Insular Experiment Station, Rio Piedras, Porto Rico, for valuable assistance in the field.

The species unrecorded from Porto Rico prior to 1926 are marked with an asterisk.

1. FULIGO SEPTICA (L.) Gmel.

   On dead wood, San Turce, Guaynabo and Rio Piedras.

2. PHYSARUM MELLEUM (Berk. & Br.) Mass.

   On leaves and twigs, Guaynabo.

3. PHYSARUM COMPRESSUM Albert. & Schw.

On leaves and twigs, Guaynabo.

*4. PHYSARUM POLYCEPHALUM Schw.

On dead wood, Hacienda Anon.

*5. PHYSARUM NUTANS Pers.

On leaves and twigs, Guaynabo.

The sporangia have unusually long stalks and delicate capillitium.

*6. PHYSARUM RENIFORME (Mass.) List.

On dead wood, Coamo Springs.

*7. PHYSARUM SESSILE Brandza.

On leaves, Guaynabo.

Miss Lister (Monog. Mycet. Ed. 3, p. 55, 1925) says that this species was formerly regarded as a plasmodiocarp form of *Physarum variabile* Rex. The Porto Rican material, which is very scanty, has lime knots and spores similar to Brandza's species, but the general appearance is not the same. It inclines more to definite sporangia, and may be *P. variabile*. Further collections are needed for positive determination.

8. DIDYMIUM SQUAMULOSUM (Albert. & Schw.) Fries.

On leaves, Guaynabo.

A variable species. Among a number of gatherings, one shows extremely long stalks.

9. DIDYMIUM NIGRIPES (Link) Fries.

On leaves, Guaynabo.

Also, a variable species. Several fruitings were found, all with dark stalks. One seems to be quite typical; another has a small, dark, rough columnella; a third has a large white columnella.

*10. DIDERMA HEMISPHERICUM (Bull.) Horne.

On leaves, Guaynabo.

*11. STEMONITIS HYPEROPTA Meylan.

On mossy log, Cidra.

This species is described by Miss Lister (Monog. Mycet. Ed. 3, p. 134, 1925) as including two small spored heretofore recognized varieties of *Comatricha typhoides* (Bull.) Rost. The Porto Rican specimen has spores 4.5 μ in diameter. The reference to *S. hyperopta* is somewhat doubtful.

12. COMATRICHA LONGA Peck.
On dead wood, Mayaguez.
*13. COMATRICHA IRREGULARIS Rex.
On dead wood, Guaynabo.
*14. LAMPRODERMA VIOLACEUM (Fries) Rost.
On mossy log, Cidra.
*15. LAMPRODERMA ARCYRIONEMA Rost.
On herbaceous stalks, Guaynabo.
*16. CRIBRARIA INTRICATA Schrad.
On dead wood, Guaynabo.
*17. CRIBRARIA VIOLACEA Rex.
On twigs, Guaynabo.
18. DICTYDIUM CANCELLATUM (Batsch) Macbr.
On dead wood, Guaynabo.
19. LYCOGALA EPIDENDRUM (Buxb.) Fries.
On dead wood, Mayaguez.
*20. OPHIOTHECA WRIGHTII Berk.
On dead wood, Guaynabo.
21. ARCYRIA DENUDATA (L.) Sheldon.
On dead wood, Guaynabo.
22. ARCYRIA CINEREA (Bull.) Pers.
On dead wood, Guaynabo, Cidra.
23. HEMITRICHIA CLAVATA (Pers.) Rost.
On twigs, Guaynabo.

MINEOLA,
NEW YORK.

NOTES AND BRIEF ARTICLES

Just as this was going to press we received an announcement of the death of Dr. Curtis G. Lloyd on Thursday, November 11, at his home in Cincinnati. Further details of his life and work will appear in a later number of MYCOLOGIA.

We learn from one of the local newspapers that Dr. John Dearness, Associate Editor of MYCOLOGIA from its beginning, has recently been awarded the degree LL.D. from the University of Western Ontario. The readers of MYCOLOGIA will doubtless all be pleased to know that this added honor has come to one of our oldest mycologists.

In Notes on Parasitic Fungi in Wisconsin XIII, there is an error on p. 172 that should be corrected. In the third line above the figure "2593" should be 3491. Fungi Columbiani 2593 was correctly labeled *Tuberculina Davisii* Sacc. & Trav. but 3491 was not. J. J. DAVIS.

A MONOGRAPH OF THE BRITISH LICHENS

The above is the title of a descriptive catalog of the species of lichens in the Department of Botany in the British Museum (Part II) by Annie Lorrain Smith, F.L.S. It is stated in the preface that the long interval between the publication of parts I and II has been caused by the continued ill-health and death of Rev. James Crombie. Miss Smith has used his manuscript and so far as possible followed his form. The book contains 447 pages of text and 63 plates showing the diagnostic characters of the species treating. This part contains the Graphidaceae and the Pyrenulaceae.

AMANITA SOLITARIA

This very large and very handsome species occurs abundantly in the dry oak woods of Virginia and adjoining states from mid-

summer until October. It is usually white and covered with powder and large warts, the stipe being concolorous and very thick at the base, where it is often prolonged into a root-like projection.

The abundance of this species at Lynchburg, Virginia, during the past two summers, which were exceedingly dry, set me to thinking and experimenting. I found that the large swollen base of the hymenophore is a water reservoir, and on this account the unexpanded pileus can endure drought for weeks, waiting for a rainy spell to continue its development.

Even after partial expansion, the covering of powder and fine scales protects the plant from drought as fine hairs protect foliage. It is also provided in most cases with a distinct odor of chlorine or chloride of lime, which keeps most insects away and allows the pileus many days in which to disseminate its spores.

It is a great pity that such a splendid mushroom is not edible. What fine messes one could have when few other mushrooms could be found! Many of the caps are over six inches broad, and only a few of them would make a meal. To be sure, it is only slightly poisonous and McIlvaine took a chance on it, but the stomachs of ordinary mortals might not be so well fortified. W. A. MURRILL.

NOTES ON FLORIDA FUNGI

Seeking a milder climate for recuperation after a severe illness, the writer spent the months of March and April, 1926, on St. Andrew's Bay in Florida. As a needed exercise in outdoor life the study of phytobiology was undertaken as more to his taste than golf or fishing.

The fungous flora of the region at that season of the year was found to be rather sparse. The few specimens observed were mostly of tough species or old and weathered specimens. Occasionally in some moist, deeply shaded hollow a prostrate tree of *Magnolia* or *Quercus* would be found bearing an abundant crop of several cosmopolitan species, such as *Stereum versicolor*, *Polyporus hirsutus* Wulf. and *Polyporus arcularius* (Batsch) Fries. The Bay is shut off from the Gulf by a long, narrow sand spit, on the inner side of which a large pine log lay partly buried in

the sand as though cast upon the shore by some storm. This bore a number of unusually large masses of *Lenzites saepiaria* Fries one of which was an imbricated mass on the end of the log, 4 × 10 × 12 cm. in size.

St. Andrew's Bay lies in what is known topographically as the coast flatwoods. The region is low, but a few feet above the sea-level. The surface is slightly undulating and so near the water-table that many of the depressions are wet or filled with shallow ponds only a foot or two deep. As the soil is chiefly a loose, porous sand through which the water readily passes, the slight elevations are commonly dry and often more or less sterile, but the depressions frequently contain a considerable accumulation of alluvium forming a rich moist loam. Under these conditions one passes in a few rods from dry sandy areas of scrub oak and pine to moist and dense almost tropical-like jungles. These latter occupying the depressions are commonly known as "titis" and are usually characterized by a dense growth of *Cliftonia*.

In several widely separated places were found specimens of *Clathrus columnatus* Bosc. which would seem, therefore, to be a fairly common species in this region for one of the Phallales or stinkhorns. The plant seems to be chiefly confined to the drier sand areas. One was found among the sand dunes along the Gulf shore. At Lynn Haven, in one dooryard of almost barren and very loose sand, these plants came up at frequent intervals for weeks and I was informed had been observed in the same spot for at least two years as they had been very annoying to the housewife on account of their disagreeable odor. The mycelium would, therefore, appear to be perennial, but it is possible that there were successive crops through seeding by means of ground beetles.

The plants, as is the case with many of the fleshy fungi, spring up more frequently after a rainy night, but "eggs" were observed apparently on the verge of eruption that passed through two or more heavy rains before the receptacle finally burst through the volva. It is evident that showers do not induce eruption until the plant has fully developed. In fact, I am disposed to think that dry weather retards the eruption more than wet weather hastens it. If the shower does not come at the opportune time

the plant soon bursts through the volva, but is less successful in the display of its characteristic features and is not so likely to attract attention. Those that opened during a dry spell were apt to be small and distorted and were frequently hindered in their erection by dried portions of the volva adhering to the receptacle.

Clathrus when fully developed is characterized by four crimson bars or columns arising from the central base of the volva, curving outward and up, then converging and finally uniting at the top in a four-sided arch on the underside of which and on the inner face of the top of the bars is the slimy spore-bearing gleba. The plant appears to be quite variable and several species have been described which are probably only growth variations. One remarkable form was observed among the plants which came up in the above described plot and doubtless from the same mycelium, otherwise we might well have supposed it to be a distinct species. Instead of four bars there were eight and theseunited at the top in pairs, forming a row of four separate arches. In another specimen two transverse bars were present, each uniting two of the vertical bars at about half their height.

If the plants are not collected within two or three hours after the volva opens there will usually be found within the receptacle several black ground beetles, apparently scarabaeids, feeding ravenously on the softer portions. Even without the aid of these beetles the plant soon decomposes and a specimen was never observed the second day after eruption. Until eruption the "eggs" are very persistent for many days regardless of the changes of weather.

In the same dry sand area were observed a number of puffballs, evidently *Astrea hygrometricus* (Pers.) Morg. and what appeared to be *Lycoperdon Peckii* Morg. Also the old base of a remarkably large *Scleroderma Geaster* Fries was found half buried in the sand and on the trunk of a prostrate palmetto was detected a cluster of sporophores of what I suppose we must consider the very common *Schizophyllum commune* Fries, although, when found in the fresh state, it was difficult to believe that this was the same plant so often seen in the North. The dried specimen,

however, assumed a more normal appearance. I have not found it recorded on palmetto.

These were practically all the larger fungi observed with the exception of several fine specimens of *Polyporus sanguineus* (L.) Fries perhaps too near the northern *P. cinnabarinus* (Jacq.) Fries but of thinner texture. HOWARD J. BANKER.